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PART 2

THE FOSSIL RAILS OF C. W. DE VIS, BEING MAINLY AN EXTINCT FORM OF TRIBONYX MORTIERII FROM QUEENSLAND

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SUMMARY

OLSON, S. L. 1975. The fossil rails of C. W. De Vis, being mainly an extinct form of Tribonyx mortierii from Queensland. Emu 75: 49-54.

The fossil rails described by C. W. De Vis from late Pliocene or early Pleistocene deposits (Chinchilla Sand) in south-eastern Queensland were re-examined. Fulica prior was found to be synonymous with F. atra. All the other rallid fossils represent an extinct form of Tribonyx mortierii, recognizable by its slightly smaller size as a distinct subspecies for which the name Porphyrio reperta De Vis has priority. The rest of De Vis's names (Gallinula peralata, G. strenuipes, Tribonyx effluxus, and Porphyrio mackintoshi) are synonymized with Tribonyx mortierii reperta, Tribonyx mortierii is believed to have evolved on the mainland and spread to Tasmania when the two were connected. At some time after the final opening of Bass Strait, the mainland population became extinct, leaving a relic on Tasmania that evolved a slightly larger size.

INTRODUCTION

Six rails named by C. W. De Vis (1888, 1892) from south-eastern Queensland provide the only fossil evidence of the Rallidae so far recorded from Australia. De Vis's work is highly unreliable; his 'descriptions are often inadequate and difficult to interpret, his figures generally poorly executed' (Bartholomai 1966: 115). Consequently, the identity of De Vis's fossil rails has been far from certain. Through the courtesy of the Queensland Museum I have been able to examine all but one of the types, as well as some additional referred material of these forms. The synonymies resulting from these studies not only greatly simplify our notion of Australian fossil rails, but shed interesting new light on the evolution of the flightless Tasmanian Native-hen Tribonyx mortierii.

THE SPECIMENS: THEIR PROVENANCE AND AGE

The first rallid specimens described by De Vis (1888: 1277) were 'yielded by the Darling Downs in the immediate neighbourhood of Chinchilla, a township 200 miles [320 km] by rail west of Brisbane. The Chinchilla deposits are beds of sand . . . about three miles from the township on the north bank of the River Condamine . . . The names Porphyrio reperta, Gallinula strenuipes and Fulica prior were introduced

in this publication. Part of the type material of *F. prior* later (De Vis 1892) became the type of *Tribonyx effluxus*; so it may be assumed that all four of these types came from the locality described above. Likewise, the referred specimens of *P. reperta* (see below) are labelled 'Chinchilla, Darling Downs.'

The species Porphyrio mackintoshi, Gallinula peralata and Tribonyx effluxus were described by De Vis in 1892. This paper was evidently intended as a continuation of the 1888 account because it is without an introduction and begins immediately with accounts of species, Unfortunately, no definite mention of localities is made and one wonders therefore if the Chinchilla locality mentioned in the introduction to the 1888 paper was intended also to apply to the specimens described in the 1892 paper.

A perhaps deceptive allusion to a locality is made in the account of *Porphyrio mackintoshi*, which species De Vis (1892: 440) 'dedicated to a gentleman who rendered most kindly aid to the collector, Mr. Hurst, during his search for fossils of this kind near Warwick.' Note, however, that there is no indication that the type itself came from Warwick, only that Mr Mackintosh was helpful in looking for fossils there. The whereabouts of the type of *P. mackintoshi* is not known. That of *Gallinula peralata* is labelled simply 'Darling Downs.'

There is a problem in that there are fossil deposits of different ages in Darling Downs, those at Chinchilla being the oldest and those in eastern Darling Downs, including the vicinity of Warwick, being younger. At least one of De Vis's fossil species (Lithophaps ulnaris) is stated definitely to have come from Warwick (De Vis 1891a), as was a femur assigned to the extinct species Uroaetus brachialis (De Vis 1891b). The only certain locality for any of De Vis's fossil rails is that at Chinchilla and the types of Gallinula peralata and Porphyrio mackintoshi could as well have come from there as elsewhere.

The deposits at Chinchilla were termed the Chinchilla Sand by Woods (1960). East of Chinchilla, also along the River Condamine, are several fossil localities in fluviatile deposits believed on the basis of their marsupial fauna (particularly Diprotodon optatus) to be Pleistocene in age (Woods 1960). The diprotodontid and macropodid faunas of the Chinchilla Sand are different from those of eastern Darling Downs. These differences are believed to signify a difference in age; the geographic proximity of the two localities and the widespread nature of the latter fauna make it unlikely that they are merely of ecological significance' (Woods 1960: 396). For these reasons Woods tentatively referred the Chinchilla Sand to the Pliocene. It seems quite possible, however, that such faunal changes could occur in the Pleistocene. Dr Mary Wade, Curator of Geology at the Queensland Museum, informs me (in litt.) that 'the youngest date that can be fastened on to Chinchilla Sand is pre-glacial Pleistocene, and we don't know vertebrate ranges well enough to tell how much older it is.' The fossil birds from these deposits that have been restudied have all proved to be referable to modern species (Miller 1966a and b; Olson this paper) and are thus not inconsistent with a Pleistocene age. No doubt most of De Vis's other fossil avian taxa can likewise be synonymized with modern forms. Thus, for the present, the most accurate age that can be affixed to the Chinchilla rails would appear to be late Pliocene or early

Some particulars of De Vis's type-specimens are summarized in Table I. In addition to these I have also examined the following topotypes identified in De Vis's hand as *Porphyrio reperta*: two left femora (QM F7007, F7008), a right tibiotarsus lacking the distal end (QM F7009), a very worn proximal right tibiotarsus (QM F1127). A distal third of a right tibiotarsus with no data but bearing De Vis's annotation 'C. fulica' was found to fit perfectly onto a proximal portion of a tibiotarsus (also with no data) identified as P. reperta by G. F. van Tets. The complete bone is now entered as QM F7030. None of these specimens was mentioned in De Vis's publications but all are rallid and all pertain to the form that ultimately comes under the name reperta.

THE DISPOSITION OF FULICA PRIOR

Fulica prior was originally based on a proximal right humerus and a distal right humerus of another individual (De Vis 1888). Later, De Vis (1892) recognized that the distal humerus was not that of a coot and made it the type of Tribonyx effluxus, leaving the proximal humerus as the type of F. prior. Most of the distinguishing characters of F. prior were actually based on the distal humerus, but De Vis did not trouble to redefine the species.

The type of F. prior is indeed from a coot but on comparison was found to be inseparable from F. atra. De Vis mentioned its smaller size, but the typespecimen falls within the lower ranges of the nominate race F. a. atra (Table II), which is consistent with the reputedly smaller size of the Australian race F. a. australis. Other alleged differences in F. prior, such as the narrower head with more convex articular surface, either are not apparent or will not distinguish the type from an adequate series of F. atra. As Miller (1966a: 185) has noted, De Vis 'evidently proceeded on the general belief that all fossils should be designated as separate species, whether or not they differed significantly from their modern relatives. Fulica prior De Vis is here synonymized with Fulica atra Linnaeus.

A MAINLAND FORM OF TRIBONYX MORTIERII Because I believe all of De Vis's remaining types and referred material to represent a single species of large flightless rail only subspecifically distinct from Tribonyx mortierii, all of these specimens are here considered together.

TABLE I
The type-specimens of fossil rails from Queensland.

Species	De Vis	Type element	QM Cat. No.		
Porphyrio reperta	1888	Distal right tarsometatarsus	F1126		
Porphyrio mackintoshi	1892	Distal right tarsometatarsus	Not at OM		
Gallinula strenuipes	1888	Left tarsometatarsus	F1128		
Gallinula peralata	1892	Right humerus	F1144		
Tribonyx effluxus	1892	Distal right humerus	F1138		
Fulica prior	1888	Proximal right humerus	F1129		

The elements of the hindlimb indicate a rail much larger and heavier than Gallinula tenebrosa, Tribonyx ventralis, Amaurornis olivaceus, Fulica atra or any of the smaller Australian rails. Although I was unable to examine a skeleton of Eulabeornis castaneoventris, the fossil tarsometatarsi are considerably larger and heavier than those in skins of that species. Furthermore, the fossil form was flightless (see below), but E. castaneoventris is not.

Compared to Porphyrio, all the fossil hindlimb elements are much more robust. The femora are longer and have much heavier and more curved shafts. The tibiotarsi, though shorter than in Porphyrio, are nearly twice as thick. The tarsometatarsus of Porphyrio is highly specialized for a rail (Olson 1973a), with the shaft greatly thinned proximally, the trochleae more nearly in the same proximo-distal plane, the scar for the hallux deeply excavated and the distal foramen large and rounded. These specializations are also evident even in the large flightless form of Porphyrio, 'Notornis' mantelli. The Oueensland tarsometatarsi show none of these characters and clearly are not referable to Porphyrio. In all of their more important features these fossil hindlimb elements agree perfectly with Tribonyx mortierii (Plates 4 and 5).

Even from De Vis's illustration, the type humerus of Gallinula peralata may be recognized as that of a flightless rail. This is shown by the low elongate

flattened head, on nearly the same level as the internal tuberosity, the greatly curved shaft, the thickened and reduced deltoid crest and the reduced bicipital crest, all of which are characters that the humeri of most flightless rails assume. The only flightless rail in Australia is *Tribonyx mortierii*, to which species the humerus of *peralata* is similar in form and length (Plate 4, Table II).

The type of Tribonyx effluxus is one of the more fragmentary, abraded and perhaps least diagnostic of De Vis's rallid types. Ridpath (1972: 118) studied this specimen and suggested that it may have come from a flightless species but he did not think that it was a 'sufficiently characteristic part of the skeleton upon which to decide the fossil's relationships.' The brachial depression is too small for Porphyrio and the shaft is too heavy for Tribonyx ventralis, Gallinula tenebrosa or Fulica atra. Except for having a more slender shaft, the specimen is very similar to the type of G. peralata and it agrees well with Tribonyx mortierii. As noted by Ridpath (1972: 118) the 'radial trochlea' (= external condyle) is somewhat more oblique to the long axis of the shaft than in T. mortierii but the difference is slight and 'the shape of the radial trochlea varies appreciably between different individuals of T. mortierii.' There is no reason to suppose that the type of T. effluxus came from a species different from the rest of the Chinchilla fossil rails.

TABLE II

Measurements (mm) of Tribonyx m. mortierii compared with T. m. reperta and of Fulica atra compared with F. prior. * = estimated.

	Proximal. Width		Least Width Shaft		Distal Width			Length				
	range	mean	s.d.	range	mean	s.d.	range	Weán	s.d.	range	Dean	s.d.
Femur mortierii (n=17)	16.9-20.0	18.3	.70	5.9-7.3	6.4	.45	15.2-18.4	17.1	. 72	78.0- 87.2	83.9	2.57
Femur reperta QM F7008	16.1			6.1			15.1			80.0		
Femur <u>reperta</u> QM F7007	16.9			6.3			15.2			72.3		
Tibia mortierii (n=16)	13.3-16.1	14.8	. 70	5.7-6.7	6.2	.40	11.6-12.9	12.4	.54	123.0-140.9	133.6	5.12
Tibia reperta QM F7009	15.1			6.5		•				128*		
Tibia reperta QM F7029	13.3			5.9			12.0			121		
Tarsua mortierii (n=11)	12.7-14.4	13.3	.76	5.3-6.0	5.7	.33	12.7-14.3	13.5	.63	75. 0- 90.7	83.1	4.86
Tarsus <u>reperta</u> QM F1128	12.6			5.6			12.1			74.6		
Tarsus reperts QM F1126				5.5			12.2			70 *		
Humerus mortierii (n=14)	13.9-15.5	14.5	.66	4.2-4.7	4.5	. 20	9.3-10.3	9.9	.26	60.7- 68.4	65.0	2.25
Humerus reparts QM F1144	14.2			5.0			10.4			62.8		
Humerus reperts QM F1138				4.5*			9.9					
Humerus <u>Fulica</u> atra (n=13)	13.5-15.8	14.8	.90	4.2-4.9	4.5	.28						
Rumerus Fulica prior	13.6			4.7						_		

The distal end of a tarsometatarsus forming the type of Porphyrio mackintoshi was apparently never placed in the collections of the Queensland Museum, and I have been unable to locate it. Although De Vis (1892: 440) compared it only with *Porphyrio* he indicated some uncertainty as to its proper placement by saying that 'it is probable that this [species] and P. reperta, m., will eventually be placed in a new genus, as in both the hind toe is less elevated than in the recent genus, and the inner trochlea (imperfect in the cotype [sic] of P. reperta) is found in the present fossil to be distinctly shorter, or rather not to extend so far distad . . .' These characters are found in Tribonyx mortierii, and along with De Vis's illustration (Plate 4, inset), show definitely that mackintoshi is not referable to Porphyrio. The only difference De Vis noted between mackintoshi and reperta was the larger size of the former. In view of the great variation in size in modern Tribonyx mortierii and in the Queensland fossil form (Table II, Plates 4 and 5), and also in view of the abundance of the latter in the Chinchilla deposits, it seems safe to assume that mackintoshi, too, belongs to the extinct form of Tribonyx mortierii.

Though all the Queensland fossil rails, except the type of Fulica prior, appear to be referable to the species Tribonyx mortierii, not all agree exactly with the modern Tasmanian form, even though there is a great deal of individual variation in the size and proportions of the elements of the limbs of modern mortierii (Plates 4 and 5). The two fossil femora are smaller than modern specimens with similar proportions (Plate 5). One of these is absolutely smaller than any modern specimen (Table II). One of the fossil tibiotarsi is inseparable from modern mortierii, but the other is just below the minimum for that form. The fossil tarsometatarsi are likewise slightly smaller than in the modern form and the proximoanterior part of the shaft in the type of strenuipes is somewhat more excavated. The fossil humeri are within the range of size of mortierii. The shaft of peralata is considerably heavier than in any modern specimen (Plate 4) but appears as if it may be from an abnormal individual. The shaft of effluxus is not any heavier than that of modern mortierii.

The differences shown by the fossils (mainly smaller size) I do not consider to be of more than subspecific value (see discussion). Of the five names applicable to the fossil form, *Porphyrio reperta* and *Gallinula strenuipes* are the two oldest and were proposed simultaneously. As first reviser, I choose reperta because of page priority and in view of the more widespread use of this name, at least in labelling specimens. *Gallinula strenuipes*, *Gallinula peralata*, *Tribonyx effiuxus*, and *Porphyrio mackintoshi* thus become synonyms of *Tribonyx mortierii reperta*.

Elsewhere (Olson 1973b), I have reduced Tri-

bonyx to a subgenus of Gallinula, but I have used Tribonyx in the present account for the sake of clarity. The extant Tasmanian Native-hen ought then to be known as Gallinula mortierii mortierii (Du Bus) and the extinct mainland form as Gallinula mortierii reperta (De Vis). For this reason I have retained the spelling reperta throughout, although if used with either Porphyrio or Tribonyx it should be rendered repertus, as already noticed by Brodkorb (1967).

DISCUSSION

Because the volant Black-tailed Native-hen Tribonyx ventralis occurs on the mainland of Australia but not on Tasmania, and because T. mortierii is found on Tasmania but not on the mainland, it has usually been thought that mortierii is an insular derivative of ventralis (e.g. Mathews and Iredale 1921). However, Ridpath and Moreau (1966) thought that the differences between them suggested that the two species had been separated for some time. The late Pliocene or early Pleistocene occurrence of T. mortierii in Queensland, documented here, not only confirms the antiquity of the separation of mortierii and ventralis, but also shows that mortierii is evidently not a Tasmanian autochthon. On New Zealand there was another flightless species, Tribonyx hodgeni, now extinct, that was nearer in size to ventralis but more similar in cranial morphology to mortierii (Olson in press). Tribonyx hodgeni probably arose from an ancestor closer to the common ancestor of both mortierii and ventralis than to ventralis itself. This is further evidence that ventralis is not a primitive or ancestral stock.

Because Bass Strait was in existence in the Miocene (Ridpath and Moreau 1966) and because T. mortierii was in Queensland before Pleistocene glaciations caused lower sea-levels, T. mortierii probably would not have evolved on Tasmania and spread from there to the continent. Successful colonization of mainland areas by insular species is rare in any case.

It is not certain just how the ancestral populations of Tribonyx in Australia became geographically separated so as to evolve into two species. T. ventralis, in any event, became more aquatically adapted and now inhabits temporary waters in semi-arid country characterized by erratic rainfall (Ridpath 1972; Ridpath and Moreau 1966). As a consequence, it is highly nomadic and retains a need for its power of flight. T. mortierii, on the other hand, became more terrestrially adapted and evidently evolved in a more equable and constant environment such as that of the present coastal areas of eastern Australia. It must have reached Tasmania when that island was connected to the mainland and was being colonized by such animals as emus Dromaius and various

In press. A review of the extinct rails of the New Zealand region (Aves: Rallidae). Rec. natn. Mus. NZ.
 RIDPATH, M. G. 1972. The Tasmanian Native Hen, Tribonyx mortierii. III. Ecology. CSIRO Wildl. Res. 17, 01, 115.

17: 91-118.

mania: ecology and evolution. Ibis 108: 348-393.
Woods, J. T. 1960. Fossiliferous and cave deposits. In
Hill, D. and A. K. Denmead (Eds.) The Geology
of Queensland. Melbourne Univ. Press. (Originally
published as Vol. 7 of J. geol. Soc. Aust.)

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large marsupials. After Tasmania was finally isolated from the mainland about 12,000 years ago (Ridpath and Moreau 1966), T. mortierii survived there but became extinct in Australia. This pattern of distribution (Fig. 1) is closely paralleled by that of such mammals as the Thylacine Wolf Thylacinus cynocephalus and the Tasmanian Devil Sarcophilus harrisi, which became extinct in pre-European times on the mainland but persisted later in Tasmania.

The larger size of \bar{T} , mortierii mortierii has probably arisen since the final isolation of Tasmania. Insular forms of many species commonly become larger than their mainland counterparts, and the differences in size between mortierii and reperta are very likely a result of this effect.

ADDENDUM

After the present manuscript had been submitted and accepted, P. V. Rich and G. F. van Tets called to my attention the fact that certain other bones among the De Vis material might be referable to Tribonyx mortierii reperta. I was able to investigate this personally and discovered a few more such bones on a recent visit to the Queensland Museum. A distal end of a right femur (QM F7022), which De Vis had labelled 'Megapodius', is from T. m. reperta (distal width 15.1 mm). A distal half of a left humerus (QM F7058) from Chinchilla identified in De Vis's hand as the fossil species 'Anas elapsa' is also from T. m. reperta. Fortunately De Vis never published on either of these two specimens. The humerus, like that of the type of 'Gallinula peralata',

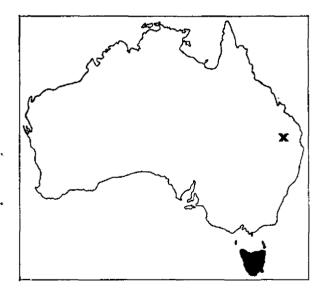


Figure 1. Distribution of the modern and fossil forms of Tribonyx mortierii. T. m. mortierii (solid) and T. m. reperta (x).

is heavier than in modern T. m. mortierii (distal width 11.0, least width shaft 5.2) so that it appears as if this may be a valid character for T. m. reperta. Two distal portions of right tibiotarsi (QM F5554 and F5555) that De Vis (1892: 444) referred to his extinct species 'Platalea subtenuis' are from T. m. reperta. These are labelled simply 'Darling Downs': the abovementioned femur has no locality data. De Vis based most of his description of Platalea subtenuis upon the proximal two-thirds of a right femur (QM F1140), which may now be regarded as the lectotype. This femur is definitely not rallid. The total number of fossils of T. m. reperta thus far identified from the De Vis material is fourteen, and these represent at least four and probably five individuals; so the species may be assumed to have been rather abundant.

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REFERENCES

BARTHOLOMAI, A. 1966. The type specimens of some of of De Vis' species of fossil Macropodidae. Mem. Qd Mus. 14: 115-126.
BRODKORB, P. 1967. Catalogue of fossil birds: Part 3

(Ralliformes, Ichthyornithiformes, Charadriiformes). Bull. Fla St. Mus. biol. Sci. 11: 99-220.

VIS, C. W. 1888. A glimpse of the post-Tertiary avifauna of Queensland. Proc. Linn. Soc. NSW (2) 3: 1277-1292

· 1891a. On the trail of an extinct bird. Proc. Linn. Soc. NSW (2) 6: 117-122.

1891b. Note on an extinct eagle. Proc. Linn. Soc. NSW (2) 6: 123-125.

· 1892. Residue of the extinct birds of Queensland as yet detected. Proc. Linn. Soc. NSW (2) 6: 437-

Mathews, G. M., and T. Iredale. 1921. A Manual of

the Birds of Australia. London: Witherby.
MILLER, A. H. 1966a. The fossil pelicans of Australia. Mem. Qd Mus. 14: 181-190.

1966b. An evaluation of the fossil anhingas of Australia. Condor 68: 315-320.

OLSON, S. L. 1973a. Evolution of the rails of the South Atlantic Islands (Aves: Rallidae). Smithson. Contribn Zool. 152: 1-53.

1973b. A classification of the Rallidae. Wilson Bull. 85: 381-416.

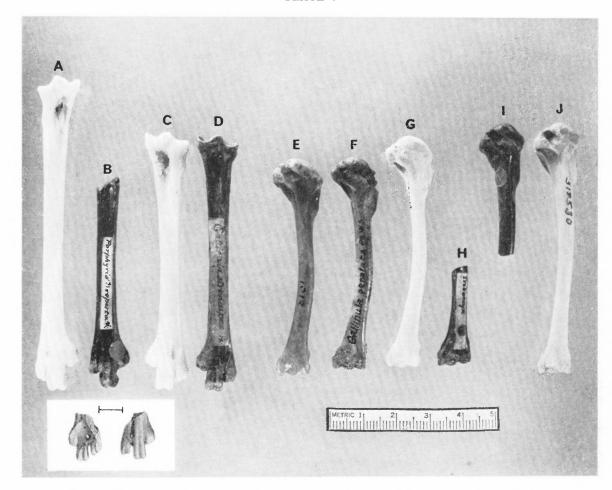


Plate 4. Limb bones of modern and fossil rails (a-d, tarsometatarsi; e-j, humeri), a Tribonyx m. mortierii (MVZ 140780); b T. m. reperta (type of Porphyrio reperta); e T. m. reperta (type of Porphyrio reperta); e T. m. mortierii (NMV B5226) note the difference from a; d T. m. reperta (type of Gallinula strenuipes); e T. m. mortierii (MR 1012; f T. m. reperta (type of Gallinula peralata); g T. m. mortierii (MVZ 140780) note difference from e; h T. m. reperta (type of Tribonyx effluxus); i type of Fulica prior; j Fulica atra atra (USNM 318530). Inset: type tarsometatarsus of Porphyrio mackintoshi (from De Vis 1892, pl. xxiv, figs 2a and 2b), scale = 1 cm.

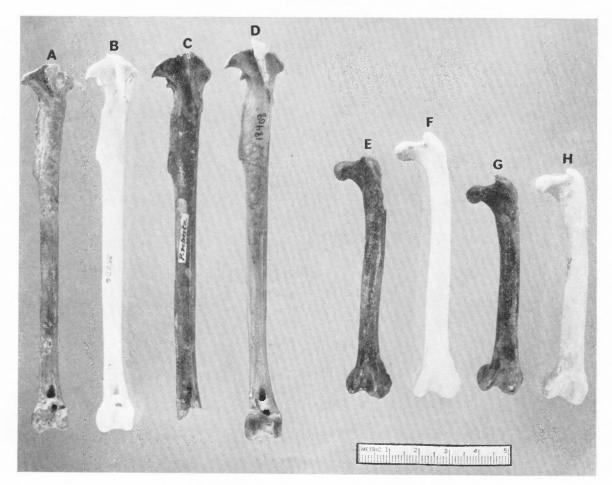


Plate 5. Limb bones of modern and fossil Tribonyx mortierii (a-d, tibiotarsi; e-h, femora).

a T. m. reperta (QM F7030); b T. m. mortierii (NMV B5226); c T. m. reperta (QM F7009); d T. m. mortierii (USNM 18408); e T. m. reperta (QM F7008); f T. m. mortierii (MVZ 140780); g T. m. reperta (QM F7007); h T. m. mortierii (NMV B5226).